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Maternal effects on tree phenotypes: considering the microbiome

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The biotic and abiotic environmental experience of plants can influence the offspring without any changes in DNA sequence. These effects can modulate the development of the progeny and their interaction with microorganisms. This interaction includes fungal endophytic communities which have significant effects on trees and their associated ecosystems. In this opinion article, we highlight potential maternal mechanisms through which endophytes could influence the progeny. We argue that a better understanding of these interactions might help to predict the response of trees to stress conditions and enhance the efficiency of tree breeding programs.

The phenotype of the tree and its endophytes

Genotype and environmental conditions during development are the strongest determinants of the phenotype of an individual tree. Although genetic and environmental conditions are dominant, in recent years accumulating evidence indicates that the biotic and abiotic environmental experience of the parents can modulate the development and pathogen-resistance of their progeny [1,2]. Specifically, maternal plants are inferred to have significantly higher impact on offspring phenotype and fitness than do paternal plants because they directly provide seedlings with a large amount of substances [3,4].

An aspect of the biotic maternal environment that might have important consequences on the phenotype of the plant, but which has hardly been explored, is the impact of associated microbial communities. There is an increasing realization that these microbial communities are an important part of the extended genotype and phenotype of the plant [5]. They can affect various aspects of the physiology, metabolism, and ecological interaction of the plants.

The importance of associations between plants and the foliar microbiome has been highlighted previously [6]; however, the mechanisms and effects of the interaction between these entities remain poorly understood. In this opinion article, we explore possible influences of endophytic fungi on trees within the context of maternal effects (Figure 1). Despite being a big challenge, research to identify the mechanisms involved in the transmission of maternal environmental effects to the progeny holds much promise to contribute to understanding plant ecology. Such information could also offer the possibility of influencing the development and resistance of plantation trees. However, before this can be achieved several challenges must be overcome in fully understanding these processes.

Maternal environmental effects on trees

Environmental maternal effects can influence the offspring without any changes in DNA sequence [7]. In plants, these effects have been reported on seed traits, germination, seedling performance, plant–pathogen, and plant–insect interactions [7–10]. Maternal effects have also been shown to attenuate the negative consequences of climate change [2]. There have been broad advances in understanding plant offspring responses to abiotic and biotic maternal environmental factors, especially within the first generation ([8] for review). However, most studies of transgenerational maternal effects on plants over several generations have focused on short-lived annuals. For example, *Arabidopsis thaliana* (*Arabidopsis*) has increased seed production under heat stress in the F_3 generation if the F_0 and F_1 experienced the same stress, and even when F_2 was grown without stress [11]. Progeny of *Arabidopsis* plants exposed to herbivores are also more resistant to subsequent attack in the next two generations, compared to progeny from unthreatened parents [12]. Available information for long-lived woody species across generations is much more limited because they do not reach reproductive maturity for decades [8,13,14].

The work of Borgman *et al.* [15] is, to our knowledge, the only study on transgenerational maternal effects in long-lived woody plant species over generations. By using twig clippings and seeds of *Pinus aristata* and *Pinus flexilis* from the same maternal plant, this study showed that the effect of the local annual weather conditions in the maternal environment over 2 years affected maternal tree twig growth, seed provisioning, and progeny performance. All these traits were positively affected by the warm dry year and negatively affected by the cold wet year. The differences in seed traits corresponded to differences in early seedling growth. However, inter-annual variation in mother tree twig traits did not predict seed mass.

Seed provisioning and epigenetic modifications are the two mechanisms through which these maternal effects are transmitted to the next generation. Seed provisioning, a mechanism in which the mother plants influences the resources allocated to seeds, is thought to affect one

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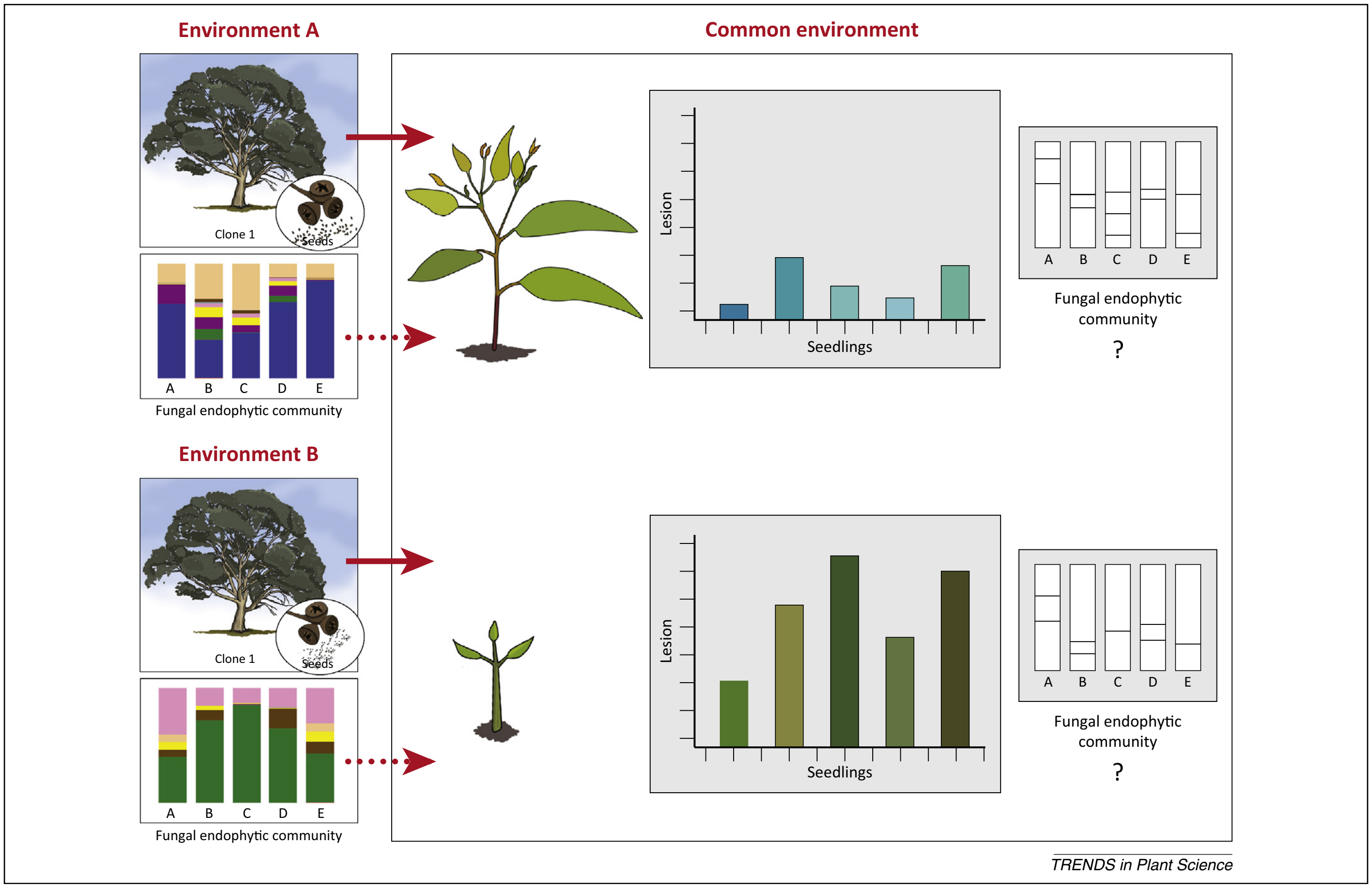

Figure 1. Hypothetical relationships between environment, fungal communities, genotype, and phenotype across two generations of trees. This picture illustrates a single mother clone in two different environments characterized by contrasting biotic and abiotic conditions. The vertical bars are the fungal endophytic community within each clone; taxonomic diversity in the fungal endophytic communities is indicated by different colors. Maternal environmental effects at a particular clone may result from different phenotypic plasticity in the seeds and even in the phenotype and resistance of seedlings growing in a common environment (continuous arrow). Seed size from maternal environment A was bigger and produced taller and more-resistant seedlings than seeds from maternal environment B. The influence of the maternal environment on the fungal endophytic community of the progeny (vertical bars without colors) is, however, unknown. Differences in the maternal fungal endophytic community should be considered as biotic maternal environmental effects. It is also important to understand to what extent these maternal fungal endophytic communities could be transferred vertically through the seeds across next generation (discontinuous arrow). If these maternal environmental or fungal community effects translate into changes in the development, resistance, and/or fungal endophytic community of the progeny, they could have important impact on ecosystems and in the management of trees in production.

offspring generation and become less relevant in maturity [3]. By contrast, epigenetic modifications are a set of molecular processes transmitted via the seeds that modulate the phenotype by modifying gene expression; these include, for example, DNA methylation, histone modification, and small RNA interference [8], and may influence the progeny for a longer time or even several generations [16].

Endophytic communities of trees

Plants comprise one of the biggest terrestrial ecosystems for microbial organisms [6], and microbial communities have colonized all plant organs. Fungi and bacteria are the most prominent members of these communities, but other phylogenetic lineages can be found (e.g., lichens [17], invertebrates [18], and viruses [19]). Bacteria and fungi grow either as phyllosphere [20,21] and mycorrhizal endophytes [22] in plant tissues, or as epiphytes [23] on plant surfaces, without causing any harmful change in the plant phenotype.

Fungal phyllosphere endophytes can, as far as has been tested, be found in all biomes, and an enormous diversity of fungal species has been documented [24–26]. A multitude of studies have shown that endophytic communities play important roles to enhance nutrient uptake, increase environmental stress tolerance, and protect the tree host from pathogens and pests (see [27] for review). Importantly, by faster population and species turnover, endophyte communities most likely respond faster to environmental changes than host plants. In fact, studies have shown that fungal endophytes may mitigate the negative consequences of environmental stresses related to climate change in agricultural and natural plant communities [28]. Although our understanding of the exact roles of different members of the endophyte community is still limited, their ubiquity, number, and diversity suggest that they are an important part of the extended genotype and phenotype of the plant [5]. As a result, the endophytic communities can have important consequences for plant fitness and therefore for plant communities and also ecosystem function.

Of equal importance is to understand how the host plant influences the associated microbiome. The effects of biotic and abiotic environmental stress and the effects of different plant genotypes on fungal endophytic communities have been studied mostly in *Arabidopsis*. The frequency